INVASION OF NORTHERN OAK WOODLANDS BY *PSEUDOTSUGA MENZIESII* (MIRB.) FRANCO IN THE SONOMA MOUNTAINS OF CALIFORNIA

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Abstract

Invasion of Northern Oak Woodland by *Pseudotsuga menziesii* [Mirb.] Franco has been observed throughout the outer North Coast Range, including the Sonoma Mountains of southern Sonoma County, California. Studies at Annadel State park, reported here, include the correlation of physical and vegetational factors with *P. menziesii* dominance. Significant negative correlations were found between *P. menziesii* seedling and sapling densities, and (1) the distance to a seed source, (2) the cover of annual grasses, and (3) total living ground cover. A significant positive correlation was found between *P. menziesii* seedling and sapling densities and the percentage of the ground surface covered by leaf litter. A significant positive correlation was also found between *P. menziesii* sapling density and the basal area of trees of any species occurring on the sample plots. Stand age analysis revealed that *Quercus* spp. found on the sample plots were consistently much older that the oldest *P. menziesii* observed. This observation also applied to sites dominated by *P. menziesii.* Surges of *P. menziesii* establishment appear to be related to changes in management of the region, including fire suppression, increased oak canopy density, and the establishment of the state park. These results suggest that events which have changed the character and dynamics of the Northern Oak Woodland within this century have in turn produced conditions favorable to the establishment of *P. menziesii.* This pattern of *P. menziesii* invasion will result in a reduction of biological diversity in this region of Northern California.

Our observations of vegetation patterns in the southern portion of the range of Northern Oak Woodland reveal an increased presence of *Pseudotsuga menziesii* seedlings and saplings beneath the oak canopy. At some locations, *P. menziesii* has grown up through the canopy and appears to be shading out the oaks. This phenomenon is in evidence at Annadel State Park in Sonoma County, California. Park management is concerned with the potential replacement of the Northern Oak Woodland by *P. menziesii* forest, particularly because

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such vegetation changes may be the direct result of the disruption of natural processes through past management.

Vegetation changes following the altering of management objectives (e.g., elimination of grazing, fire suppression, termination of wood cutting) have been documented for a number of vegetation types in coastal California (McBride and Heady 1968; McBride 1974; Elliot and Wehausen 1974; McBride and Stone 1976; Hektner and Foin 1977; Barbour et al. 1993). Comparatively little work has been done on changes in oak woodland/mixed evergreen forest in the California coast range. Wells (1962) concluded that chance is the major factor controlling the distribution of oak and other vegetation types in the San Luis Obispo area following fire. Waring and Major (1964) demonstrated a close correlation between certain environmental variables and the distribution of various vegetation types in the redwood region of Humboldt County. Griffin (1977) and Plumb and McDonald (1981) reviewed the general ecology of several oak woodland types in California. Their review did not, however, develop a comprehensive analysis of vegetation dynamics in these types. Sawyer et al. (1977) described the grassland-woodland-forest mosaic of the north coastal region as poorly understood and in need of investigation.

Several recent studies have focused on the oak woodland and hardwood forests in Sonoma County with particular reference to Annadel State Park. Anderson and Pasquinelli (1984) described the northern oak woodland at several sites along a moisture gradient within the county, including two sites in Annadel. They concluded that high oak canopy densities and lack of oak regeneration may result in the future dominance of mixed evergreen forest species at the more mesic end of the gradient. Tunison (1973) investigated the distribution of oak woodland and mixed evergreen forests on Bennett Mountain in the park. Noting the dominance of young *P. menziesii* and *Umbellularia californica* in the understory of many oak-dominated stands, he tentatively concluded that all of these oak types are seral to mixed evergreen forest. Tunison further suggested that this recent invasion of *P. menziesii* and *U. californica* is the result of the development of a closed oak canopy due to previous management. Barnhart (1978) has suggested a similar vegetation change, although he points out that the complex nature of the coast range vegetation makes it difficult to document successional trends. Wainwright and Barbour (1984) demonstrated the diverse nature of the mixed evergreen forest in Annadel, including the invasion of oak woodlands by *P. menziesii.* They did not develop any conclusions relative to successional relationships.

The encroachment of *P. menziesii* into the northern oak woodland has been demonstrated throughout the North Coast Ranges (Reed and Sugihara 1987; Sugihara and Reed 1987; Keter 1987). These and other investigators (e.g., Wills 1991) have concluded that the principle reason for this encroachment is the drastic reduction in fire frequency since 1900. Frequent fires in presettlement times presumably maintained a more open woodland and eliminated *P. menziesii* seedlings before they became large enough to be fire resistant. Recently Finney and Martin (1992) have documented mean fire intervals in the oak woodlands of Annadel State Park from 6.2 to 23.0 years with over two-thirds of the records showing intervals of less than 10 years. These short fire intervals, dating back at least four centuries before settlement, are attributed primarily to the use of fire by Native Americans.

This paper reports the evidence regarding the variables influencing the establishment of *P. menziesii* within the oak woodlands in Annadel State Park. The objective of this study was two-fold: (1) to determine the correlation between selected site variables, both physical and vegetational, and *P. menziesii* regeneration, and (2) to demonstrate the sequence of *P. menziesii* and oak establishment through stand-age analysis of mixed stands of the principle taxa.

Study Area

Annadel State Park is located immediately east of Santa Rosa, Sonoma County, California, in the Sonoma Mountains. This north-south trending range, primarily composed of Pliocene Sonoma Volcanics above older sediments (Jenkins 1951), is in the eastern portion of the county ca. 30 km from the Pacific coast. Climate patterns are typically Mediterranean, with mild winter temperatures (January mean daily minimum 2–3°C) and hot summer temperatures (July mean daily maximum 28–29°C) which are often moderated by morning fog. Total annual precipitation is ca. 750 mm/year with dry summers and wet winters (January mean 150 mm) (U.S. Weather Bureau 1964).

The vegetation of the park, typical of that found throughout the southern North Coast Range, is a complex mosaic of communities including coastal prairie, chaparral, northern oak woodland, and mixed evergreen forest (Munz and Keck 1950). Mixed evergreen forest occurs on northerly slopes and in moist drainages throughout the park, integrating with northern oak woodland, particularly in the center of the park. Northern oak woodland is predominant in the southwestern two-thirds of the park, although tree densities and composition vary with aspect. *Quercus garryana* occurs in relatively high densities on north-facing slopes, while south-facing slopes support more open savannas of oak hybrids (*Q. xexplingii*) as well as *Q. douglasii, Q. kelloggii* and *Q. agrifolia.* Chaparral occupies relatively small areas, usually on southern or western exposures and rock outcroppings. The prairie and grassland communities form small to fairly extensive meadows throughout the park. It is important to note that these vegetation types form a mosaic; areas occupied by a given type are often small and boundaries between types often abrupt.

Historically, the area in which Annadel is located was extensively utilized by European settlers and their descendants (Futini 1976). Major types of activities included cattle ranching which began in the 1830s and was the dominant activity from 1930 to 1970. Cobblestone quarrying around the turn-of-the-century and extensive cutting of hardwood for cordwood and charcoal in the 1920s also occurred. These activities ceased when the park was established in 1972.

Methods

1. Factors Influencing *P. menziesii* Regeneration

Thirteen large *P. menziesii* trees (>80 cm DBH) occurring in oak woodlands were selected from a population of over 100 similar trees observable on aerial photographs. Trees selected were at least 300 m away from any other tree chosen and a similar distance from any stand of *P. menziesii.* Each isolated tree was located on the ground and was used as a center around which sampling points were located. Four directional zones based on compass readings (NE = 0 to 90°; SE = 90 to 180°; SW = 180 to 270°; NW = 270 to 360°) were established around each tree. Each of these directional zones was divided into five concentric arcs 30 m wide. An initial sampling point was located in each of the four direction zones by choosing a random azimuth and a random distance (from 0.5 to 30 m) from the large *P. menziesii.* Subsequent sampling points within that directional zone were established at 30 m intervals along the same random azimuth. This procedure, which was repeated for each of the thirteen large *P. menziesii* trees, was adopted to insure that plots would be located at varying distances up to 150 m and in varying directions away from a *P. menziesii* tree of seed producing age. Using this procedure, 20 sampling points were located around each large seed tree selected for a total of 260 sampling points.

At each sampling point the percentage of ground cover was estimated from a 10 m^2 plot. Ground cover categories estimated were annual grass, perennial grass, broad-leaved herbaceous plants, ferns, leaf litter, base of tree, limbs and logs, rocks, and bare ground. Tree seedlings (plants <1 cm in diameter at ground level) were counted on 10 m^2 plots and saplings (plants >1 cm in diameter at ground level and <1.4 m tall) were recorded from 100 m^2 plots centered at the sampling point. Percent intercept of shrubs was determined using the line intercept method along two diagonal lines connecting opposite corners of each 100 m^2 plot.

The point-centered quarter method (Cottam and Curtis 1956) was used to determine tree density and basal area around each plot center. The distance from each plot center to the nearest *P. menziesii* tree in each of three diameter ranges (10–19.9 cm; 20–39.9 cm; and greater than 40 cm DBH) was also measured. Topographic conditions (aspect, percentage slope) were recorded at each sampling point.

The field data were used to establish correlations between each variable measured and (1) seedling density and (2) sapling density of *P. menziesii.* Pair-wise scatterplots were run between every possible combination of dependent variable (*P. menziesii* seedling and sapling density) and independent variable (percent ground cover in each category, total living ground cover, percent shrub cover, topographic condition, and distance to each diameter category of seed tree) in order to gain a preliminary understanding of the relationships among the variables. Subsequently, correlation analysis was used to determine the degree of association between these variables. Log (base 10), square root, and arcsine transformations were applied to the data in order to improve the linearity of the relationship (Sokal and Rohlf 1981). All correlations were tested at the 0.05, 0.01 and 0.001 significance levels.

Linear correlations were also determined between seedling and sapling densities and (1) the density (number/ha) of each tree species and (2) the basal area (m^2/ha) of each species. Log (base 10) transformation was applied to the data in order to improve the linearity of the relationships. The "closest" individual method (Cottam et al. 1953) was used to calculate tree density and basal area. This method uses the distance (D) from the plot center to the nearest tree as a basis for calculating density and basal area. We modified this method by measuring the distance to the nearest tree of each species. A correction factor ($2 \times D$) proposed by Cottam and Curtis (1956) was applied to the distance measurement.

2. Stand-Age Analysis

The ages of trees on sites exhibiting different *P. menziesii* height classes were determined. The region of Annadel State Park currently experiencing various stages of *P. menziesii* encroachment into oak woodlands was surveyed and specific sites were identified which exhibit the range of *P. menziesii* dominance from understory to overstory. Twenty-five plots were established which included five plots in each of five *P. menziesii* height classes:

"A" plots *P. menziesii* saplings beneath healthy oak canopy
"B" plots *P. menziesii* extending into, but not above, healthy oak canopy

"C" plots	*P. menziesii* forming a more or less open canopy above healthy oaks
"D" plots	*P. menziesii* forming a well-developed canopy above declining oaks
"E" plots	*P. menziesii* well above dead or dying oaks

The plots ranged in area from 100 to 1000 m^2 depending on tree density to assure the sampling of an adequate number of trees. About 30 trees per plot was considered an adequate number for the study. The position of each tree within each of the twenty-five plots was indicated on a coordinate plot map and assigned a number. All stumps, downed and dead trees were also marked on the plot map. The diameter at breast height was measured for all trees over 1.4 m in height. Ground level diameters and heights were recorded for trees less than 1.4 m tall. Tree age was determined from ring counts on increment cores taken at breast height and adjusted for the number of years for seedlings to reach that height based on the growth rates of seedlings and saplings in the plots. Sapling sized trees were aged from cross-sections cut at 3 cm above the ground.

Results and Discussion

1. Factors Influencing Regeneration

The first series of correlation analyses identified several statistically significant correlations between the independent variables and the density of *P. menziesii* seedlings or saplings. These correlations shown in Table 1 are for simple linear correlations. Scatter diagrams for each relationship often suggest a curvilinear rather than a linear relationship between the independent and dependent variables (Fig. 1A, B). The low correlation values (r and r^2) are due, in part, to the difficulty of fitting a straight-line to a curvilinear distribution. Low values are also frequently encountered in studies involving multiple-factor analysis due to the stochastic nature of natural processes. "Square root", "arcsine" and "log 10" transformations of the data were applied in an attempt to improve the correlations. Slightly higher values were obtained and additional relationships were shown to be significant or significant at higher levels with these transformations. However, both r and r^2 values remained relatively small ($r < 0.35$; $r^2 < 0.13$). These small values are nonetheless useful indicators of vegetation and site factors which control the invasion of oak woodlands by *P. menziesii* at Annadel State Park.

The negative correlation found between the distance to large (>40 cm DBH) *P. menziesii* trees and the density of *P. menziesii* seedlings and saplings suggests the importance of seed source in the invasion of oak woodlands by *P. menziesii.* The scatter diagrams (Fig. 1A, B) depict a curvilinear relationship which is typical of dispersal

TABLE 1. CORRELATION ANALYSIS OF INDEPENDENT AND DEPENDENT VARIABLES (*PSEUDOTSUGA MENZIESII* SEEDLING AND SAPLING DENSITY) RELATING TO *PSEUDOTSUGA MENZIESII* ESTABLISHMENT IN OAK WOODLANDS AT ANNADEL STATE PARK. (P values with the same superscript are significant at the following levels: a ≤ 0.05, b ≤ 0.01, c ≤ 0.001)

Independent variables	Dependent variables					
	Seedlings			Saplings		
	r	r^2	P value	r	r^2	P value
Seedlings and saplings of other species:						
Total no. seedlings	0.157	0.025	0.011[a]	−0.092	0.008	0.140
Total no. saplings	0.009	0.001	0.881	−0.037	0.001	0.557
Total no. seedlings and saplings	0.107	0.011	0.086	−0.088	0.008	0.154
Distance to nearest *Pseudotsuga menziesii* of three sizes:						
10–19 cm, DBH	−0.079	0.006	0.267	−0.055	0.003	0.489
20–39 cm, DBH	−0.126	0.016	0.058	−0.046	0.002	0.489
≥40 cm, DBH	−0.230	0.053	0.000[c]	−0.183	0.034	0.005[c]
Ground cover (%):						
Annual grass	−0.148	0.022	0.017[a]	−0.156	0.024	0.012[a]
Perennial grass	−0.105	0.011	0.090	−0.116	0.014	0.062
Forbs	−0.014	0.001	0.824	−0.011	0.001	0.864
Ferns	−0.048	0.002	0.437	−0.053	0.003	0.393
Bare soil	−0.010	0.001	0.872	−0.048	0.002	0.437
Base of tree	0.043	0.002	0.494	0.170	0.029	0.006[b]
Leaf litter	0.201	0.040	0.001[b]	0.205	0.042	0.001[b]
Rock	0.019	0.001	0.763	0.040	0.002	0.521
Log	−0.056	0.003	0.369	−0.072	0.005	0.245
All living	−0.216	0.046	0.000[c]	−0.224	0.050	0.000[c]
Shrub cover	−0.045	0.002	0.470	−0.037	0.011	0.553
Aspect	0.080	0.006	0.198	0.012	0.000	0.852
Slope	−0.108	0.012	0.081	−0.027	0.001	0.668

patterns for wind-disseminated propagules (Wolfenbarger 1959; Roe 1967; Harper 1977). The failure to demonstrate statistically significant correlations between seedling or sapling density and smaller *P. menziesii* trees (<40 cm DBH) may be due to the lower seed producing capacities of smaller and younger trees. Open grown *P. menziesii* trees begin producing appreciable amounts of seeds between their 20th and 30th years, but maximum seed production occurs between the ages of 200 and 300 years (Isaac 1943). As will be shown later, most of the *P. menziesii* on our sample sites are less than 50 years old.

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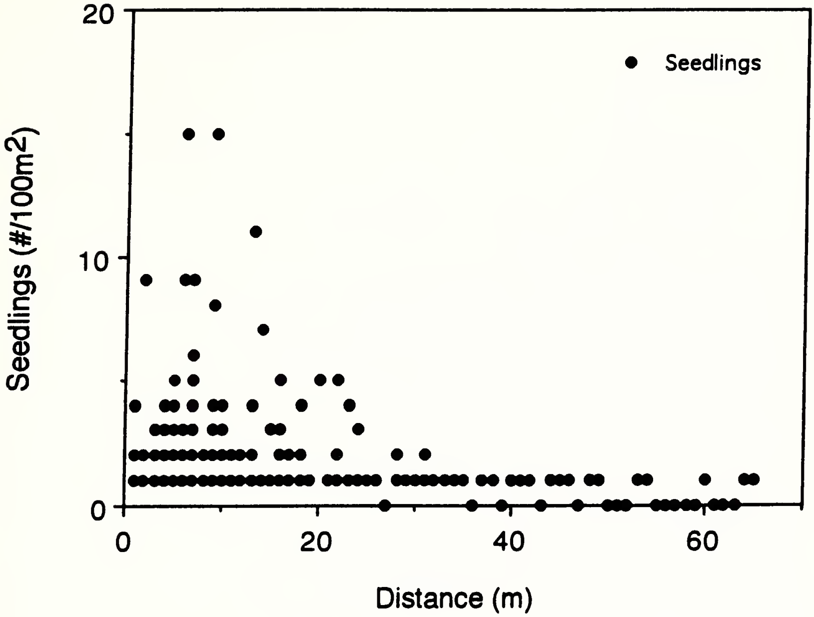
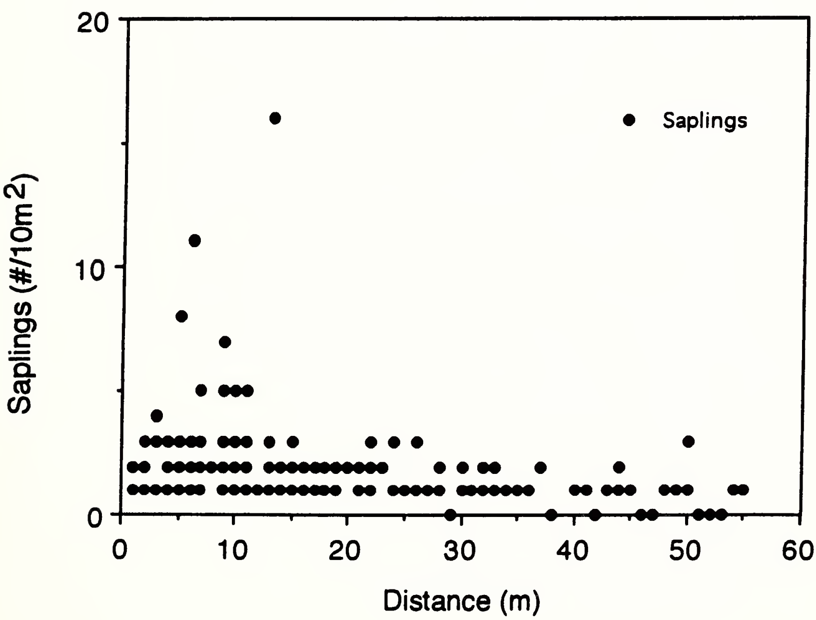
FIG. 1. Relationship between the number of Douglas-fir seedlings (A) and saplings (B) on 10 m^2 quadrats and the distance to the nearest Douglas-fir tree >40 cm DBH.


20
10
0
Seedlings (#/100m2)
Seedlings
0
20
40
60
Distance (m)


20
10
0
Saplings (#/10m2)
Saplings
0
10
20
30
40
50
60
Distance (m)

The correlation between the density of *P. menziesii* seedlings and the total number of seedlings of other tree species (Table 1) suggests that conditions favorable for the establishment of *P. menziesii* seedlings are also favorable for the establishment of other tree species. This contrasts with the findings of Isaac (1938, 1940) that high densities of *P. menziesii* seedlings are not associated with high densities of other species in the Pacific Northwest. However, *P. menziesii* establishment in the oak woodlands of Mediterranean climatic regions may be restricted to sites where other species can also regenerate. Favorable sites for all species may require understory and overstory conditions which reduce soil moisture depletion and evaporative stress during the late spring and early summer.

The various statistically significant correlations between the percentage of different ground cover types and the densities of *P. menziesii* seedlings and saplings are interpreted as indicators of the importance of soil moisture and its rate of depletion for the establishment of *P. menziesii* within the oak woodland. The negative correlations between (1) annual grass and (2) all living ground cover and *P. menziesii* seedling and sapling densities are interpreted as indicators of the importance of competition for soil moisture in the establishment of *P. menziesii.*

The positive correlation between leaf litter and the densities of *P. menziesii* seedlings and saplings can also be interpreted in terms of moisture availability and reduced evaporative stress since the larger the area covered by leaf litter on the sample plots, the smaller the cover by living plants. This would suggest reduced competition for soil moisture. Higher percent cover by leaf litter is also associated with greater crown cover. Increasing tree crown cover, which we believe was stimulated by the coppicing of the oak woodland in the period from 1900 to 1920, suggests a reduction in evaporative stress over the seedbed. A sensitivity to drought and higher levels of evaporative stress by *P. menziesii* seedlings has been suggested by several authors (Munger 1927; Isaac 1938, 1949; Isaac and Dimock 1958; Fowells 1965).

Finally, a positive correlation exists between the base of tree parameter (i.e., at least a portion of a tree base of any species within the sampling area) and *P. menziesii* sapling density, but no significant correlation is found relative to seedling density (Table 1). This suggests that seedlings can become established under proper moisture and understory conditions, but that survival into the sapling stage requires further environmental amelioration afforded by the presence of trees which provide shade. Foresters have used the term "nurse trees" for those trees which create suitable microclimates for the growth of young trees (McBride 1978).

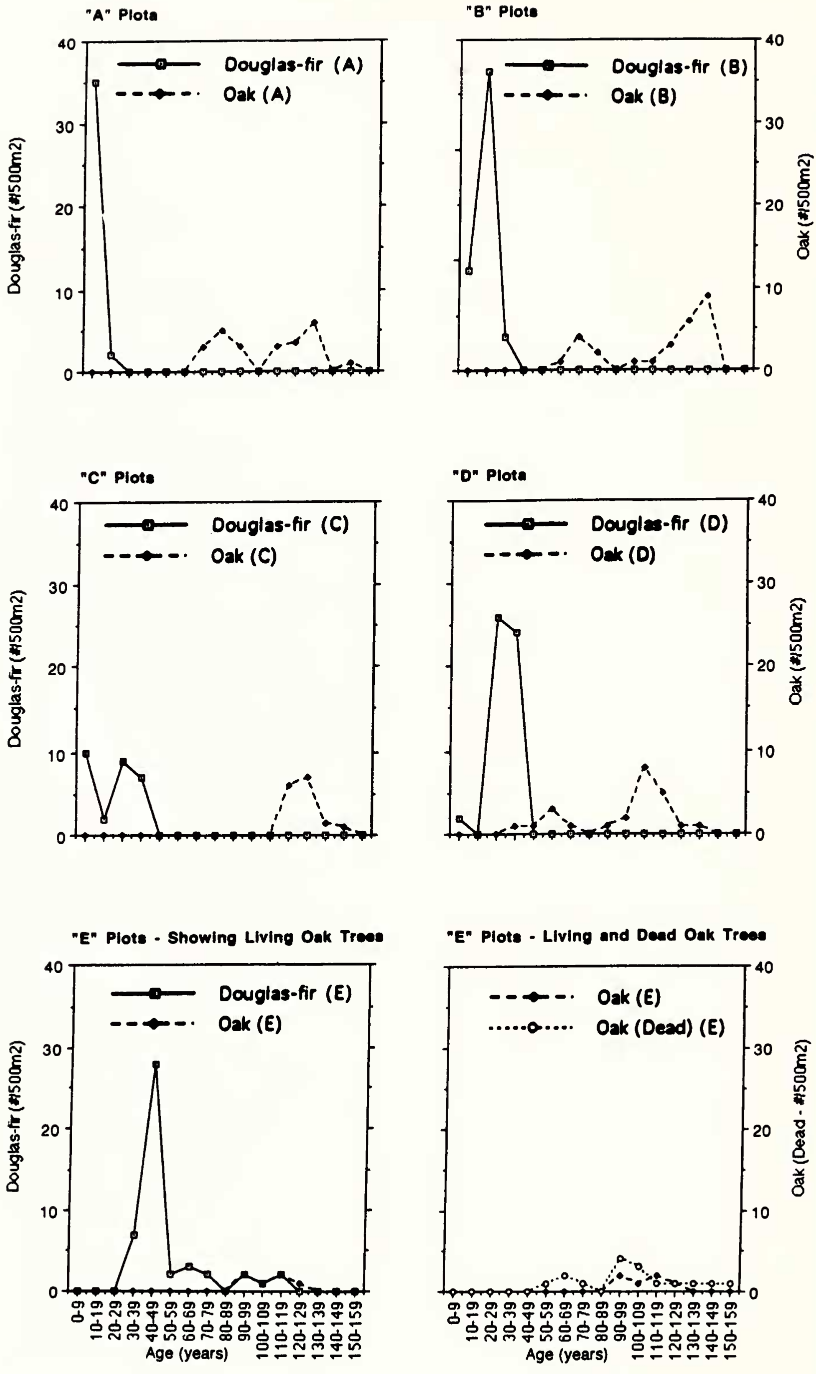
The second series of correlations was intended to measure the relationship between each tree species in the overstory and the presence of *P. menziesii* seedlings and saplings. No significant correlation was established between either the density or the basal area of any individual tree species and *P. menziesii* regeneration. Correlation coefficients were extremely low for non-transformed data. A slight improvement in the correlations was achieved by transformation of the data to log (base 10). This suggests, as was the case with the previous series of correlations, that the relationships between the dependent and independent variables are not linear relationships.

The highest r^2 value obtained for combined seedlings and saplings could account for only about 1 percent of the variation in the *P. menziesii* regeneration. It is concluded, therefore, that no single species serves as a more important "nurse tree" for *P. menziesii* regeneration than any other. Correlations were run between the basal area and density of deciduous and evergreen hardwood species and the total density of seedlings and saplings of *P. menziesii.* The r^2 values for the correlation for evergreen trees where the independent variables were basal area and tree density were 0.00003 and 0.00005, respectively. Similar values for deciduous trees were 0.0006 (Basal Area) and 0.0042 (Density).

2. Stand-Age Analysis

The numbers of *P. menziesii* and oak trees in each 10 year age class (0–9, 10–19, 20–29, etc.) for the five plot types are shown in Figure 2A–E. Oak individuals are consistently older than *P. menziesii* individuals in all plots. Only in the "E" plots (largest *P. menziesii* and dead or dying oaks) do *P. menziesii* individuals exceed fifty years, and there are very few of these older trees. In contrast, few oaks are younger than sixty years of age, with many over one hundred years old.

The composite age distribution for *P. menziesii* from all plots and the annual precipitation for Santa Rosa from 1890 to 1985 are shown in Figure 3. This figure illustrates that *P. menziesii* regeneration has been more or less continuous since 1910. No significant correlation was found between annual precipitation and regeneration for the period from 1910 to 1985. However, significant positive correlations were found when shorter, more recent time periods were examined. For the period 1973 (the year after cattle were removed from the park) to 1985 significant positive correlations were found between regeneration and precipitation from April to June ($r = 0.26$), March to September ($r = 0.29$), and the hydrologic year ($r = 0.27$) in which establishment took place. Correlations between these precipitation parameters and the number of trees established for the periods 1940 to 1985 and 1946 to 1985 were not significant. Many factors could have contributed to tree mortality over those longer periods. One


"A" Plots
Douglas-fir (A)
Oak (A)
"B" Plots
Douglas-fir (B)
Oak (B)
"C" Plots
Douglas-fir (C)
Oak (C)
"D" Plots
Douglas-fir (D)
Oak (D)
"E" Plots - Showing Living Oak Trees
Douglas-fir (E)
Oak (E)
"E" Plots - Living and Dead Oak Trees
Oak (E)
Oak (Dead) (E)
Douglas-fir (#/500m2)
Oak (#/500m2)
Oak (Dead - #/500m2)
0
10
20
30
40
Age (years)
0-9
10-19
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159

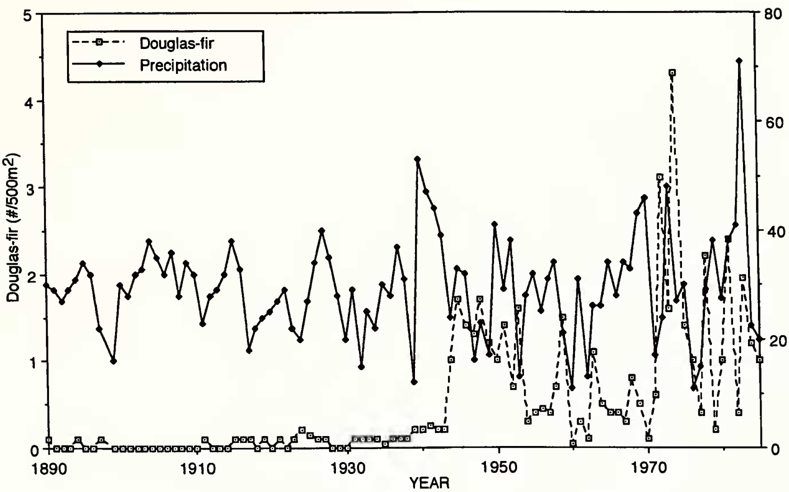


FIG. 3. Annual precipitation and establishment of Douglas-fir in oak woodlands at Annadel State Park.

would not expect to be able to demonstrate correlations between the precipitation parameters and tree establishment over such long periods. The correlations found for the more recent period support the conclusion of the study of factors (i.e., annual grass, all living plant cover, and litter cover) influencing *P. menziesii* regeneration. That is, moisture availability is an important factor in *P. menziesii* seedling establishment.

The *P. menziesii* age distribution data exhibit surges of establishment which may be related to factors other than precipitation. The abrupt increases in *P. menziesii* establishment in the early 1940s and the early 1970s are of particular interest. The surge in establishment in the early 1940s may have been a response to improved fire detection and suppression on the West Coast during World War II with the organization by the Office of Civilian Defense of the Forest Fire Fighters Service, the use of prison inmate labor, and the introduction of improved technology for fighting wildfires (Pyne 1982). The 1940's cohort of *P. menziesii* may also reflect the improved condition of seedling establishment as the oak canopy closed some 20

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FIG. 2. Age distribution of Douglas-fir and oak on plots at Annadel State Park. A = "A" plots (Douglas-fir saplings beneath healthy oak canopy), B = "B" plots (Douglas-fir extending into, but not above, healthy oak canopy), C = "C" plots (Douglas-fir forming a more or less open canopy above healthy oaks), D = "D" plots (Douglas-fir forming a well-developed canopy above declining oaks), and E = "E" plots (Douglas-fir well above dead or dying oaks).

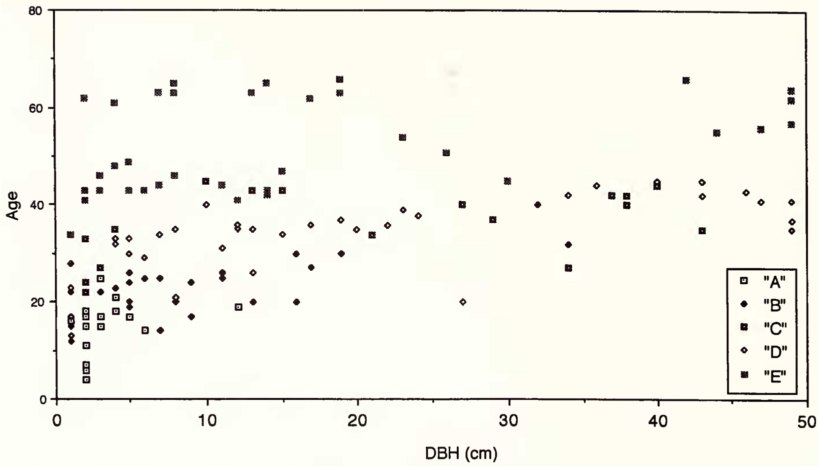

FIG. 4. Diameter range of Douglas-fir by age and plot type in oak woodlands at Annadel State Park.

years after the firewood harvesting in the 1920s. Crown closure of the oak woodland would contribute to those factors which were found to correlate positively with *P. menziesii* seedling and sapling density. This relationship is clearly illustrated by the data in Figure 2D. A lag time of about 20 to 30 years occurred between the peak of oak establishment (presumably from sprouts following extensive firewood harvesting in the 1920s) and the surge of *P. menziesii* regeneration. Similar surges in *P. menziesii* regeneration did not follow the peak of oak establishment in the 1880s (Figure 2D). Failure of *P. menziesii* regeneration following crown closure in the first decade of the 20th century was probably due to land management practices which included intensive grazing and some burning.

The second surge of establishment followed the establishment of the Park in 1972 and may be the result of the elimination of livestock combined with above average precipitation in 1972 and 1973 and an increased seed supply. *P. menziesii* trees established in the early 1940s would have been old enough to contribute to the seed supply during the surge of regeneration in the early 1970s.

The diameter (DBH) range of *P. menziesii* relative to age and type of plot sampled is shown in Figure 4. Two phenomena are clear from this analysis. First, the *P. menziesii* in a given plot type (A through E) are generally clustered into fairly distinct age groups (i.e. youngest in A plots and oldest in E plots). Of greater interest is the great disparity in diameters of trees of approximately the same age. Particularly in those plots exhibiting greater *P. menziesii* dominance (C, D and E) tree sizes are poorly correlated with age. This suggests that many older trees remained suppressed in the understory for several decades while a few trees of the same age class assumed dominance and overtopped the hardwoods. The data suggests that these suppressed trees will die unless they break through the overstory within 40–50 years.

CONCLUSIONS

Pseudotsuga menziesii has become established in oak woodlands at Annadel State Park over the past 100 years as evidenced by the stand age analysis study. No statistical correlation could be established between annual seedling establishment and precipitation for the entire period from 1890 to 1985. However, a significant positive correlation was found between the number of trees established and the precipitation for the hydrologic years from 1973 to 1985. Within this span of years significant positive correlations were also found between the number of trees established and precipitation from April to June and from March to September. Two major periods of establishment occurred in the early 1940s and the early 1970s. These two surges of seedling establishment began in years of above average rainfall. The initial surge of seedling establishment (1943 to 1953) may have resulted, in part, from improved fire detection and control initiated in World War II. The second surge of seedling establishment (1972 to 1975) corresponds to the establishment of the Park and elimination of intensive livestock grazing. Fire control and an increased seed supply from the cohort of *P. menziesii* established in the 1940s would also have been factors of importance to the second surge of establishment. *Pseudotsuga menziesii* regeneration was highly correlated with the distance to larger *P. menziesii* trees. Obviously seed source is important in regeneration. Large *P. menziesii* trees release great quantities of seeds which drop to the ground in decreasing numbers with distance from the tree. Many sites were observed where a single old *P. menziesii* had given rise to a group of smaller trees which were currently adding to the local seed supply. The resulting pattern is suggestive of islands of *P. menziesii* trees emerging through the oak woodland canopy around an older "founding" veteran. Although *P. menziesii* trees can distribute seeds up to distances of 1200 to 1400 feet (Isaac 1938), effective dispersal is probably more on the order of two times the height of the tree.

Several interesting correlations were demonstrated between the density of *P. menziesii* seedlings and saplings and site characteristics. In general, those characteristics which one would associate with more mesic site conditions and less competition for soil moisture were positively correlated with *P. menziesii* regeneration. These site conditions all suggest that increased *P. menziesii* establishment within the oak woodlands has coincided with increased density and canopy closure of the woodlands. This change in the structure of the woodlands coincides in turn with dramatic changes in the fire-regime of the park area around the turn of the century and oak-wood harvesting.

The fire history of Annadel State Park (Finney and Martin 1992) indicates that fires were both widespread and frequent before 1900. Kniffen (1939), Stewart (1951) and Barrett (1952) concluded that Pomo Indians, whose territory included the Park, burned grasslands annually. According to Kniffen, fires set annually by the Pomo maintained the oaks in open "park-like" stands. Not all annual fires set in the grasslands and savannas would be expected to burn over all of the adjacent woodlands. Thus "islands" of periodic oak establishment were maintained which would remain non-favorable to the more shade-tolerant and less fire-tolerant *P. menziesii.*

This study provides evidence that *P. menziesii* is exhibiting a rapid invasion of oak woodlands at Annadel State Park. Some areas studied show clear evidence of the growth of *P. menziesii* through the crown canopy of the oak woodland followed by the suppression and death of the oaks. Succession to *P. menziesii* forest in all oak woodland stands currently exhibiting *P. menziesii* seedlings and saplings in the understory has been questioned by a few foresters in Northern California (Pete Passoff, U.C. Cooperative Extension; Jack Marshall, California Department of Forestry and Fire Protection). They contend that similarly established *P. menziesii* regeneration usually succumbs to attacks of bark beetles and branch cankers during drought years. They have pointed to recent mortality (during the 1987–1992 drought) and mortality following the drought of 1976–1977 near Covelo, California as evidence that *P. menziesii* established on marginal sites in oak woodlands will not persist to succeed the oak woodlands. These marginal sites are characterized by clay layers in the subsoil which result in perched water tables and restrict deeper penetration of *P. menziesii* roots. During drought years these perched water tables dry up leaving the *P. menziesii* regeneration stranded in a layer of very dry soil.

Field observations at Annadel State Park and over an extensive area to the east in Sonoma and Napa counties have not identified areas of *P. menziesii* mortality beneath or within the canopies of oak woodlands during the period of drought beginning in 1987. These observations combined with the differences in soils between Annadel State Park and the Covelo area indicate that the invading *P. menziesii* seedlings and saplings will not disappear. Similar conclusions have been derived from studies in the "bald hills" of Redwood National Park, Humboldt County (Reed and Sugihara 1987) and in southwestern Trinity County (Keter 1987).

Taken collectively, these data suggest that a number of environmental factors, including fire, have been instrumental historically in keeping the woodlands open, thus encouraging the establishment of oak rather than *P. menziesii.* The lack of fire in these sites during the past fifty years plus other factors which have specifically encouraged the development of denser oak woodlands have collectively provided for the establishment of *P. menziesii* in areas of Annadel State Park where this species has not historically occurred. These trees have grown large enough in forty to fifty years to crown-out and kill the adjacent oaks, yet most of the *P. menziesii* of similar age remain small, suppressed and will eventually die as well. This pattern of *P. menziesii* establishment in oak woodlands will continue in this region as long as fire is excluded and woodlands remain unusually dense. Eventually *P. menziesii* will come to dominate many areas now supporting stands of Northern Oak Woodland. Loss of these woodlands in the mosaic of vegetation types will lead to an overall reduction in biological diversity in Annadel State Park and elsewhere.

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